RELATIVE GROWTH IN POGONA (REPTILIA: LACERTILIA: AGAMIDAE)

G.J. WITTEN

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The growth of a group of captive-bred Pogona brevis was studied over a period of a year. The data collected from these individuals were compared with data from other species of the genus, and two species from closely related genera. P. brevis has a shorter tail and limbs than other members of the genus. P. minor has three subspecies which differ from each other to a similar extent as most other species. In the case of P. minor minima this probably reflects adaptation to a different ecological niche. Mainland specimens placed in P. m. minima by Badham (1976) because of morphological similarities were indistinguishable from other P. m. minor morphometrically. The intraspecific variation within P. minor helps confirm the long maintenance of an East-West cline in the species. Enough data from P. minor and P. vitticeps were collected to analyse growth changes after sexual maturity was attained. For some measurements there were distinct changes in relative growth rates at maturity while others changed little. There were differences between the two species in which proportions were affected. These differences affect correlation coefficients, and it was unclear whether data collected from a small group of individuals over time were better indicators of relative growth patterns than data from museum specimens from scattered localities. All species within the genus differ morphometrically in some features. Morphometric data have proved useful in taxonomic decisions from intergeneric to subspecific levels. Reptilia, Agamidae, Pogona, relative growth, morphometrics.

G.J. Witten, Department of Anatomy and Physiology, Royal Melbourne Institute of Technology, Plenty Road, Bundoora, Victoria 3083, Australia; 15 October 1993.

Many contributions to agamid taxonomy have employed body proportions. Earlier contributions used simple arithmetic proportions (e.g. Storr, 1966), but Badham (1976) employed allometric data of tail length to help distinguish between *P. barbata* and *P. vitticeps*. Witten (1985) compared relative growth of a large number of agamid lizards, and found phylogenetic relationships at the generic level were supported by allometric data. Johnston (1992) used allometric analyses to help distinguish *Ctenophorus tjantjalka* from closely related species.

Three features of allometric change have been suggested as significant indicators of evolutionary relationships. Huxley (1932) suggested that allometric coefficients might act as important phylogenetic indicators; Gould (1977) emphasised the conservatism of early development, and considered juvenile proportions were better phylogenetic indicators; Dodson (1975) thought that ecological constraints would influence relative growth, particularly in animals lacking parental care.

The work by Witten (1985) certainly provided support for Gould; related species were more similar in body proportions as juveniles than as adults. These data provide less support for

Huxley's suggestion of similar allometric coefficients in related species. The lack of detailed ecological work means that Dodson's hypothesis remains effectively untested. Witten's study was preliminary. Most data came from museum specimens, and for most species data were compiled from animals collected over a wide area, from different populations. Allometric data for some species were based on as few as 12 specimens, and the analyses were thus limited to rather crude estimates. This was enough to allow broad comparisons to be drawn, and to infertaxonomic and phylogenetic relationships, particularly at higher levels. In the absence of a greater data base it has been difficult to assess whether the inferences drawn by Witten were justified.

Melbourne Zoo recently (1990) bred a clutch of downs bearded dragons (*Pogona brevis*). These animals presented the opportunity to gather data from a series of closely related specimens over a growth period. As part of a taxonomic revision of the genus data were collected for the other species in the genus, largely from museum specimens using methods similar to Witten (1985). An assessment of the methodology used by Witten (1985) is therefore possible. The enlarged data base also allows an extension

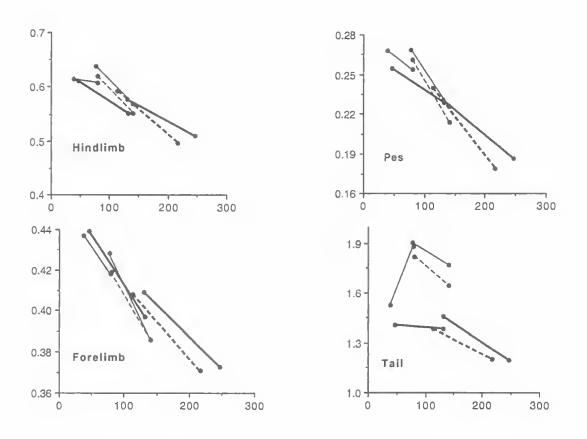


FIG. 1. Relative lengths of appendages in *P. minor* and *P. vitticeps* showing changes at sexual maturity. Male and juvenile data represented by unbroken lines, females by broken lines. The lines extend over the observed size range for each category. *P. vitticeps* grow larger, and are represented by thicker lines. All measurements are plotted as ratios of the snout-vent length against snout-vent length, to emphasise the changing ratios, but each line is calculated from the least squares regression of logged data.

of the use of allometric data. A number of issues need to be addressed: 1, Witten (1985) made no attempt to examine possible sexual dimorphism and how this related to allometric changes. The large amount of data collected from *Pogona minor* allow this area to be explored; 2, previously animals from different localities and possibly different populations were used to calculate relative growth of species. This can now be compared to data collected from siblings during growth, and the validity of lumping data from several populations may be assessed; 3, allometrie data from a congenerie group of species could be compared with the broad approach taken by Witten (1985). He found differences useful in separating generic level groups, but closely related species showed less variation in allometry. Recent work has confirmed the phylogenetic position of *Pogona* between *Ctenophorus* and *Amphibolurus* (Witten, 1994), so comparisons with *Ctenophorus nuchalis* and *Amphibolurus norrisi* were made to examine the generic definitions. The variety of taxa within and near *Pogona* now allow comparisons between subspecies, closely related species, congeners not closely related, as well as species from closely related genera. This should allow an assessment of the utility of relative growth data in taxonomie and phylogenetic studies.

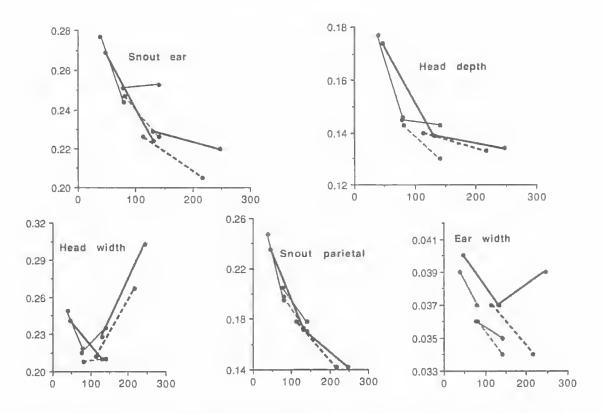


FIG. 2. Head proportions of P. minor and P. vitticeps to show changes at sexual maturity. Lines as for Fig. 1.

MATERIALS AND METHODS

Limb, tail and shout vent lengths were measured to the nearest 0.5mm using a perspex mounted ruler. Other measurements were recorded using dial callipers accurate to 0.05mm. Where possible, measurements were recorded on both sides of the body and the mean used in analyses. Head depth was recorded at the centre of the orbit. Pes length was taken as the distance from the base of the claw on the fourth toe to the furthest point of the tarsus with the ankle fully flexed. Morphometric data were analysed as in Witten and Coventry (1990), with logged data regressed by the least squares method to calculate Huxley's allometric formula. The calculated regression lines were used to illustrate allometric changes over the observed size range for each taxon, although the data were converted to ratios of snout vent length in figures to emphasise differences between groups of data.

RESULTS

INTRASPECIFIC COMPARISONS

The large amount of data collected to compare mainland 'minima' morphs with typical P. m. minor and P. minor minima (see below) allowed a more detailed analysis of growth. The sex of all adult P. minor is easy to tell by the activity of the preanal and femoral glands, with males having more active glands and consequently wider pores with more secretion (Witten, 1994). Animals of adult size were sexed as they were measured, mainly by examination of gonads, but also by examination of pores where the abdominal cavity was not open, and the morphometric data analysed for both sexes. Smaller animals were treated as a single class to give a growth calculation up to the size at which sexual maturity is normally attained. Data for P. vitticeps collected to establish the taxonomic status of smaller specimens from the Victorian mallee (Witten & Coventry, 1990) allowed similar analyses to be carried out for that species. There were insufficient data for the other species to be analysed in this way.

In most measurements there is a shift in the rate of allometry at sexual maturity (Figs 1, 2). The single exception is forelimb length (Fig. 1), where there is little change, and there is little sexual dimorphism. For the hindlimb and pes data, the negative allometry characteristic of the genus in these meas-

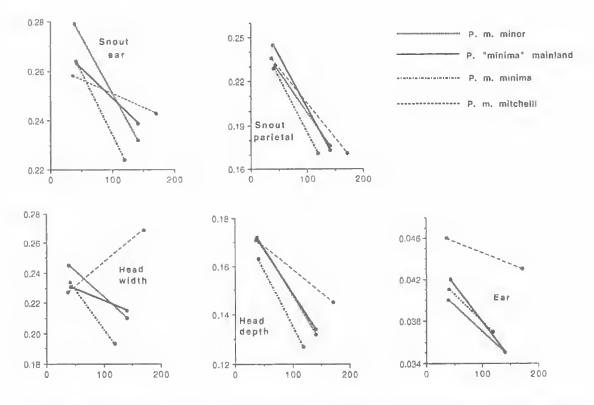


FIG. 3. Head morphometric data of *P. minor*. Each line represents the least squares regression line over the recorded size range for each population or subspecies, but converted to ratios as in Fig. 1.

urements accelerates at sexual maturity for *P. minor*, although this is not pronounced in *P. vit-ticeps*. Tail length in *P. minor* increases rapidly during juvenile growth, but decreases in both sexes after sexual maturity. Males have relatively longer tails, but this is apparently achieved during early growth, and is simply maintained after sexual maturity (Fig. 1).

All head measurements show negative allometry during growth, as is typical of vertebrates (Gould, 1977). At sexual maturity, however, this trend is at least slowed. In male *P. minor* there is positive allometry of head width and the snout-ear interval after maturity, suggesting a larger head not present in females (Fig. 2). In *P. vitticeps* ear width increases after maturity in males, but not females, and both sexes have strong positive allometry of head width (Fig. 2). In both species juvenile negative allometry for the snout-parietal interval and head depth is slowed, but there is little sexual dimorphism.

Large males of most Australian agamids develop 'jowls', an expansion around the posterior

part of the head. The positive allometry of head width is therefore not unexpected for male P. minor. P. vitticeps are characterised by a wide head, and the positive allometry of both sexes in this species is also unremarkable. What is not immediately apparent from casual observation is that males tend to have larger heads overall than females, particularly in P. minor. The length, as indicated by the snoutear measurement, and the depth of the head, are greater in larger males than females of similar size (Fig. 2). With this additional data it is apparent that head width is not dissimilar to other head measurements, and 'jowls' may not have influenced head width measurements significantly. The wider ear aperture of male P. vitticeps was also not detected in other analyses, nor is it obvious from casual observation.

SUBSPECIFIC COMPARISONS

Pogona minor was originally described as a subspecies of *P. barbata* (Sternfeld, 1919), as was *P. minima* (Loveridge, 1933). Badham (1976) treated both as full species, and described the related *P. mitchelli*. Storr (1982) reduced the latter two taxa to

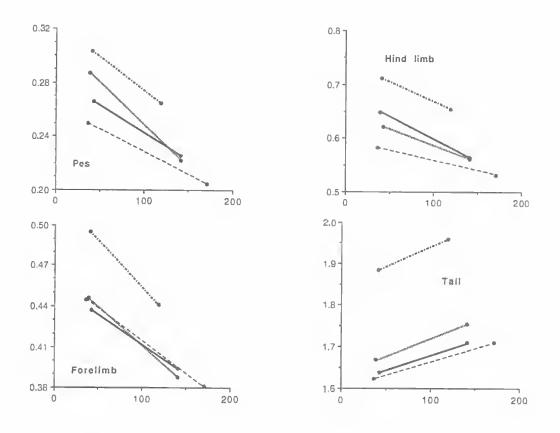


FIG. 4. Appendage morphometric data of P. minor. Lines as for Fig. 3.

subspecies of *P. minor*. Storr also restricted *P. m. minima* to the type locality of the holotype, the Houtman Abrolhos Islands. Originally *P. m. minima* included some specimens from the mainland adjacent to the Houtman Abrolhos, and Badham had assigned *Pogona* from the south west corner of Western Australia to *P. minima*.

Badham (1976) used the presence of a 'distinct nuchal row of 5 or 6 spines parallel to and on either side of the vertebral column' as the main feature characterising *P. minima*. Using this character, I sorted mainland specimens into 'minima' morphs and *P. m. minor*. Animals intermediate in morphology or distribution (following Badham's boundaries between the taxa) were excluded from these analyses.

Analyses of the resulting morphometric data indicate that mainland 'minima' morphs are much nearer P. minor than P. m. minima. P. m. mitchelli diverges strongly from the other populations in the possession of a much wider head, as originally described by Badham (1976), and also has a slightly deeper head at its maximum size than other *P. minor* (Fig. 3). The width of the ear opening is wider in *P. m. mitchelli* at all sizes. *P. m. minima* differs from other *P. minor* in developing a slightly smaller head, best illustrated in the snout-ear and head width measurements. *P. m. minima* differs from other *P. minor* more markedly in the length of its appendages (Fig. 4), with longer tail, hind limb and forelimb at all sizes. *P. m. mitchelli* tends to have a shorter hind limb than both the 'minima' morphs and typical *P. minor*, but is similar in tail and forelimb length (Fig. 4).

SPECIES COMPARISONS

Head width data show some dramatic differences between taxa. There are considerable differences in the relative head widths of juveniles, but the remarkable data are in the development of relatively wide heads in the adults of some taxa. *P. vitticeps*, as suggested by its specific name has

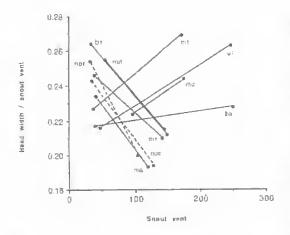


FIG. 5. Head width data for *Pogona*. Lines drawn as for Fig. 1. Unbroken lines: ba = *P*. barbata; br = *P*. brevis; mc = *P*. microlepidota; mr = *P*. m. minor; ma = *P*. m. minima; mt = *P*. m. mitchelli; nul = *P*. nullarbor; vi = *P*. vitticeps. Broken lines: nor = Amphibolurus norrisi; nuc = Ctenophorus nuchalis.

a very wide head, achieved through strong positive allometry of head width (Fig. 5). However, *P. m. mitchelli* has a relatively wider head than *P. vitticeps*, and *P. microlepidota* is similar to *P. vitticeps* in both relative head width and in the allometric changes. The other 'giant' *Pogona*, *P. barbata*, maintains a relatively wide head throughout growth, in contrast to the negative allometry of all other taxa (Fig. 5).

Head depth is similar in juveniles of all species studied, but becomes relatively deeper in *P. m. mitchelli* and *P. microlepidota* (Fig. 6). Remarkably little variation occurs in the other head measurements. For snout-parietal (Fig. 7) and snout-ear (Fig. 8) distances most *Pogona* achieve similar adult ratios, although at a much larger size in *P. vitticeps* and *P. barbata*. *P. brevis* differs in the juvenile ratios of both these measurements, but this may be an artefact of having data from very small specimens (see Discussion).

P. m. minor, P. m. minima and P. vitticeps have a narrower ear aperture than other Pogona (Fig. 9). Other taxa, including P. m. mitchelli, have higher ear width measurements. P. nullarbor is the only species with marked allometry in this measurement, strong negative allometry taking it from the 'wide ear' group as a juvenile to the 'narrow ear' group as an adult.

Hind limb length decreases with growth in all species measured. There are some large dif-

ferences within *P. minor*. *P. m. mitchelli* has the shortest hindlimb of all taxa measured, while *P. m. minima* has longer hind limbs than all but *P. microlepidota* (Fig. 10). The results for the last species need to be treated with caution, as there were very few specimens available for study. Of the other taxa in *Pogona*, there is more variation among the juvenile measurements than those at larger sizes, with *P. brevis* having the second longest hind limbs as hatchlings after *P. m. minima*. *P. nullarbor* and *P. brevis* have stronger negative allometry than other *Pogona*.

The pes length contributes to the total hind limb measurement, and not surprisingly analyses of pes length parallel those for the hind limb (Fig. 11). *P. m. minima* and *P. microlepidota* are again above the main group of *Pogona*, *P. brevis* and *P. nullarbor* have a relatively shorter pes at their maximum size.

P. m. minima and P. microlepidota, both outstanding because of high hind limb and pes measurements, also have longer forelimbs than other Pogona (Fig. 12). P. brevis has longer forelimbs as juveniles, but at adult size falls within the main group. Only P. nullarbor, with slightly shorter adult forelimbs varies from this main group of Pogona species (Fig. 12).

Variation in tail length within *Pogona* allows the genus to be split into three. No species has strong allometry, but *P. brevis* has a much shorter tail throughout its size range (Fig. 13). *P. nullarbor*, *P. vitticeps* and *P. barbata* form an intermediate group, while the subspecies of

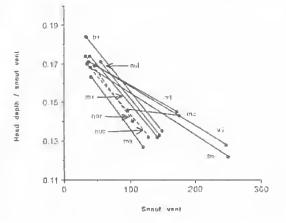


FIG. 6. Head depth data for *Pogona*. Lines and abbreviations as for Fig. 5.

| Measurment | P. brevis (n=86) | P. minor (n=86) | P. vitticeps (n=70) |
|----------------|---------------------|--------------------|------------------------|
| Head width | 0.988 | 0.960 | 0.973 |
| Snout parietal | 0.984 | 0.977 | 0.987 |
| Snout car | 0.993 | 0.976 | 0.989 |
| Head depth | 0.983 | 0.965 | 0.984 |
| Ear width | 0.958 | 0.873 | 0.954 |
| Tail length | 0.985 | 0.949 | 0.977 |
| Hind limb | 0.987 | 0.979 | 0.992 |
| Pes length | 0.978 | 0.962 | 0.980 |
| Forclimb | 0.990 | 0.986 | 0.991 |

TABLE 1. Correlation coefficients (r2) for regression calculations of three species of *Pogona*.

P. minor and *P. microlepidota* form a third group with longer tails (Fig. 13).

INTERGENERIC COMPARISONS

Both species included for comparison with *Pogona* resemble *P. m. minima* in head width. As juveniles both *Amphibolurus norrisi* and *Ctenophorus nuchalis* have slightly wider heads, but have relatively narrower heads than all *Pogona* as adults (Fig. 5). For head width the two non-*Pogona* species fall within the range of typical *Pogona*, differing only from those *Pogona* species with larger heads. In head length, however, *A. norrisi* has a longer snout-ear interval than most *Pogona*, while *C. nuchalis* develops a shorter snout-ear interval during growth (Fig. 8). This difference is not as apparent in the snout-parietal measurement, but the same trend is present (Fig. 7).

The ear width measurements reflect the development in *Pogona* of a sunken tympanum. *Ctenophorus nuchalis* has a superficial tympanum which is probably not significantly smaller than the tympanum in *Pogona*, but the ear width measurement in the latter is really a measure of the size of the opening to the auditory meatus, not a measure of the tympanum itself. *Amphibolurus norrisi* retains the sunken tympanum of *Pogona*, and differs little in this measurement (Fig. 9).

Amphibolurus norrisi has very long hind limbs, including the pes, relative to most Pogona, but relatively short forelimbs. Ctenophorus nuchalis, however, is nested among the 'typical' Pogona for all limb measurements (Figs 10-12). Similarly, the tail is long in A. norrisi, but the tail of C. nuchalis is shorter than all Pogona but P. brevis.

SAMPLE COMPARISONS

The measurement of a clutch of lizards over a growth period provided a large amount of data from a small sample of closely related animals. This is a strong contrast with the data of Witten (1985), and for the data from other species in this study.

Data from a similar number of *P. minor* were compared with the data from *P. brevis*. Most of the *P. minor* data were taken from South Australian specimens, and an attempt was made to use specimens of a similar size distribution. The correlation coefficients from the two sets of data were compared (Table 1). As might be expected, the *P. brevis* data had higher correlation coefficients than the data from *P. minor*. Data from 70 *P. vitticeps* were also compared with the other sets of data. These data, like those from *P. minor*, came from specimens from a wide area, but unlike the *P. minor* data, had correlation coefficients higher than the *P. brevis* data for some measurements (Table 1).

The comparatively high correlation coefficients for *P. vitticeps* data when compared with data from other species is surprising. In the light of the discussion above, this might be interpreted as indicating *P. vitticeps* has evolved more recently, and has not developed the intraspecific variation which characterises *P. minor. P. vitticeps* might also be less variable because it occupies a narrower range of habitats. These are possible explanations, but the answer is more likely to lie with changes in relative growth of *P. vitticeps* after maturity. Differences in allometry at maturity in *P. vitticeps* are less pronounced

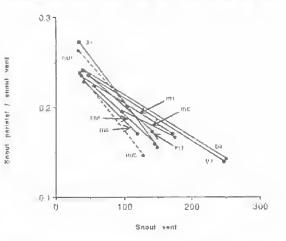


FIG. 7, Snout-parietal data for *Pogona*. Lines and abbreviations as for Fig. 5.

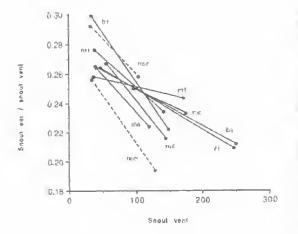


FIG. 8. Snout-car data for Pogona. Lines and abbreviations as for Fig. 5.

than in *P. minor*, allowing a better fit of the calculated curve to the real data (Figs. 1, 2). The *P. vitticeps* data have lower correlation coefficients for measurements where relative growth changes more sharply at maturity, including head width and tail length. In measurements where there is little change in relative growth at maturity, as in hind limb length, the correlations are higher relative to both other measurements and to the data of *P. brevis*.

DISCUSSION

Previous publications using morphometric data of agamids have not included an analysis of growth before and after sexual maturity. The analysis done here comparing these features of growth in P. minor and P. vitticeps indicate it is a potentially valuable method. However, differences in relative growth after sexual maturity need to be treated with some caution. There is the very real possibility that the recorded differences reflect a 'relative growth' equation derived from different sized adults, rather than sexually mature adults which were still growing. This 'relative growth' would thus be more similar to mammals than most reptiles. In mammals, determinant growth means that population differences may be analysed to show differences in the adult form. For example, deer antlers become relatively larger in large species (Gould, 1977). Pogona may have a growth pattern approaching determinant growth. Four adult male P. brevis were measured twice, first in October 1990 and again in July 1991. They varied in size from 123 to 147mm snout-vent length on the first occasion, and from 128 to 148 on the second. These animals were mature for some time before their first measurement, so variation in adult size may not indicate age. The data for *P. vitticeps* were certainly affected by differing adult size, as they include measurements from both the small southern form as well as the more widespread 'giant' form (Witten & Coventry, 1990). To gather data free of this problem would require measuring the same animals as they grew to full adult size. There would then be the further complicating factor of determining when sexual maturity had been reached.

Whether or not differing adult size was due to growth after maturity or a longer juvenile growth phase, some sexual dimorphism is apparent from the data presented here. Males have larger heads, indicated by several measurements. Male Pogona may engage in physical territorial contests (pers. obs.), apart from displays such as head-bobbing. It would be interesting to investigate whether increased head size in males led to increased reproductive success, and whether this was related to physical encounters or ritualistic displays. Sexual dimorphism in snakes is closely correlated to the presence of male combat, with species exhibiting male combat having larger males (Shine, 1994). There is some variation in male behaviour within Australian agamids. Males of Amphibolurus nobbi (Witten, 1974) and Ctenophorus fordi (Cogger, 1978) apparently lack territorial behaviour, and the presence or absence of similar dimorphism in those species would therefore be of interest.

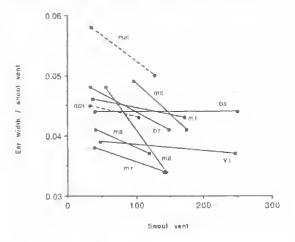


FIG. 9. Ear width data for Pogona. Lines and abbreviations as for Fig. 5.

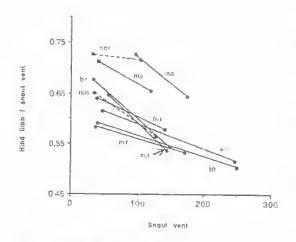


FIG. 10. Hind limb length data for *Pogona*. Lines and abbreviations as for Fig. 5.

The differences observed between the sexes do suggest that any differences between the sexes ideally should be minimised or eliminated before making interspecific comparisons. However, there is little difference in limb proportions between the sexes of the two species with adequate data, nor are there large shifts in allometric rates of change at sexual maturity for these features (Fig. 3). While there is no guarantee that this holds for the other species studied, it is likely that interspecific differences recorded in these measurements are not greatly affected by sexual dimorphism.

It should be pointed out that the methods used here to illustrate morphometric differences were deliberately chosen to highlight small differences. The data presented by Witten (1985) came from a much wider group of lizards, and many species analysed there would be off the scale of the figures presented in this paper. The data presented there were used to illustrate broad differences between species of different genera, often adapted to very different niches. However, morphometric data are useful in analysing differences

even subspecies.

The variation within *P. minor* is remarkable. In head size in general, and head width in particular, *P. m. mitchelli* is less similar to the type species than *P. vitticeps*, so named because of its wide head. This remarkable diversity of form fits within the one breeding population, as there is little doubt that these subspecies intergrade in the north west of Western Australia (Storr, 1982; Witten, 1994).

The intraspecific differences within P. minor are similar to those between other species of the genus. One aspect of this variation is that P. m. minima, from islands off the West Australian coast, is quite different morphometrically to otherwise similar specimens from the adjacent mainland. Badham (1976) placed mainland specimens in the species minima, which Storr (1982) reduced to a subspecies of P. minor, and restricted to specimens from the Houtman Abrolhos Islands. Morphometric data support Storr's position. There is a morphological cline from east to west in mainland P. m. minor with far western specimens very similar to P. m. minima (Witten, 1994). It seems the continued gene flow between mainland populations has had the effect of preventing major changes in body proportions. The interruption in gene flow by marine barriers has apparently allowed P. m. minima to differentiate morphometrically.

The maintenance of a cline within *P. minor* appears to be the result of different selective pressures operating within the range of the species. Animals from the south west are apparently evolving toward the more arboreal habitat preference of the *Amphibolurus* radiation, while those of central Australia resemble other species of *Pogona* from arid habitats (Witten, 1994). The mainland population clearly interbreeds, maintaining gene flow between the aridand mesic-adapted morphs. However, gene flow between *P. m. minima* and the mainland populations has clearly been interrupted by rising sea levels. The effect of a recent interruption to continued gene flow on morphometric evolution is

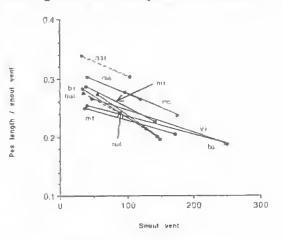


FIG. 11. Pes length data for *Pogona*. Lines and abbreviations as for Fig. 5.

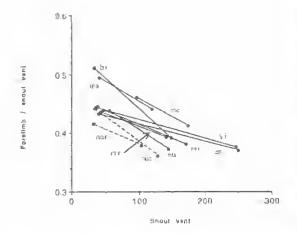


FIG. 12. Forelimb length data for *Pogona*. Lines and abbreviations as for Fig. 5.

remarkable. All mainland *P. minor* retain very similar juvenile proportions (Figs 3, 4), even when there are marked differences as adults, such as in head width (Fig. 3). *P. m. minima* appears to have been freed from this early conservatism, as it differs in a number of proportions throughout growth, but particularly in tail and limb lengths (Fig. 4). There are possible explanations apart from interruption to gene flow, but this is the most obvious factor relevant to the situation.

Variation within P. minor is of interest from several perspectives. Witten (1985) suggested morphometric differences were of sufficient phylogenetic importance to base genera on them. While the differences within *P. minor* are not of the same magnitude observed between different genera, they are significant, and cast doubt on the presumed conservative nature of such characters. If significant differences occur within populations of one species, this may indicate an ability to quickly evolve significantly different allometric features. Other data, however, point to a long maintenance of variation within P. minor. P. m. minima shares morphological features with both Chlamydosaurus and members of the Amphibolurus radiation, and it is probable that these taxa share a common ancestor (Witten, 1994). On this basis, it seems likely that variation within one species has persisted while other descendants from the original population have radiated out to form several new genera, and a large oumber of species. If this is true the morphometric variation within P. minor is less surprising.

Witten (1985) compared morphometric data from only *P. barbata* and *P. vitticeps*. The choice of these two species from the perspective of variation within the genus was unfortunate, as they are very similar in most measurements. This similarity does not appear to indicate a close phylogenetic relationship, as *P. barbata* is clearly nearer *P. nullarbor*, and *P. virticeps* is near *P. minor* (Badham, 1976; Witten, 1994). It could be that the large size attained by these species places constraints on the relative proportions of the animals, in the way hypothesised by Dodson (1975). In support of this idea, the oext largest species of the genus, *P. microlepidota*, is also similar to the two giant species in several measurements, although not all.

P. brevis differs from other species in many of its juvenile proportions (see especially Figs 6-8). This is contrary to the expectations of Gould (1977), who predicted more similarity in closely related taxa, and to the findings of Witten (1985) who demonstrated more similarity in juvenile proportions than in other morphometric data of agamids. The data for P. brevis, however, differs somewhat from those of other species, in that there were a number of very small individuals, down to 33mm snout-vent length. In other species few small specimens were examined, and none as small as the smallest P. brevis. The steep changes in ratios during early growth may produce large differences in the calculated measurements for the smallest P. brevis. The apparent differences between the smallest P. brevis and other species is more likely to be the result of using data from very small specimens than any large difference in juvenile proportions.

Morphometric data from Amphibolurus norrisi and Ctenophorus nuchalis were compared with data from

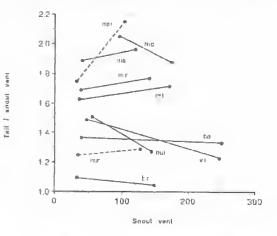


FIG. 13. Tail length data for *Pogona*. Lines and abbreviations as for Fig. 5.

Pogona. It is clear from morphological data that the former has derived from an animal resembling P. minor (Witten, 1994), and the latter shares some derived features with Pogona, and may be similar to its ancestor (Witten, 1982). Morphometric data are consistent with these hypotheses. In most features there is at least one taxon within Pogona which closely resembles one or other of these species. Ctenophorus nuchalis and its relatives differ from other Ctenophorus species groups in possessing a short blunt head, and very short limbs (Witten, 1985). These features are very similar in P. brevis and P. nullarbor, more so than other members of the genus. It is interesting to speculate that this indicates these species are more primitive within the genus. A distinctly longer tail has evolved in P. minor and P. microlepidota, a feature shared with Amphibolunus. This may represent a derived character within Pogona, and indicate a relationship to Amphibolurus. However, this should be considered speculative. Selective pressures may shift body proportions quite rapidly, if the differences in P. m. minima are taken as an indication. The conservation of body proportions in mainland P. minor is probably the result of continuing gene flow from a large arid-adapted population to a comparatively small mesic-adapted population rather than any innate conservatism. Morphometric analyses usually support relationships inferred from other data, however, and may be useful where other such data are lacking.

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APPENDIX

Specimens examined:

- Pogona barbata: AMR17904, AMR20987, AMR21578, AMR25789, AMR59988-90, AMR59992, AMR107397, AMR107399-405, AMR107407-8, AMR107411-3; QMJ49966; NMVD137, NMVD151, NMVD723, NMVD744, NMVD896, NMVD966, NMVD1345, NMVD7934, NMVD8038, NMVD14034, NMVD14036, NMVD14679, NMVD14699, NMVD48900, NMVD57127.
- Pogona brevis: AM field series 11238, 11240; QMJ32292, QMJ38735, QMJ38760-2, QMJ46949; NMVD11164-5; WAMR9856.
- Pogona microlepidota: WAMR43028, WAMR44258, WAMR46847, WAMR46962, WAMR56232, WAMR57108.
- Pogona minor: AMR15182, AMR5660-1, AMR7658; NMVD493, NMVD2657, NMVD2979, NMVD3010, NMVD3037, NMVD3052, NMVD65339, NMVD65361, NMVD65379; SAMR322, SAMR587, SAMR1402A-D, SAMR4820, SAMR5312, SAMR6556, SAMR9520, SAMR14482, SAMR14635, SAMR14955A-C. SAMR14986A-C, SAMR15004A-D, SAMR15304, SAMR15506, SAMR15568-9, SAMR18132-3, SAMR18168-9, SAMR18376, SAMR21374, SAMR22914-5, SAMR24479, SAMR25427-8, SAMR25673, SAMR26389, SAMR26809, SAMR28437, SAMR28525, SAMR29903, SAMR30083, SAMR31872, SAMR26389, SAMR31916, SAMR31923, SAMR31939-40, SAMR31961, SAMR31989, SAMR32011, SAMR32019, SAMR32036-8, SAMR32073, SAMR32076, SAMR32095, SAMR32142, SAMR32146, SAMR32165, SAMR32174, SAMR32189, SAMR32205, SAMR32214, SAMR3218, SAMR32279, SAMR32288, SAMR32312, SAMR32613, SAMR32622, SAMR33983, SAMR36226, SAMR37656; WAMR19568, WAMR31004, WAMR34182, WAMR34197-8, WAMR45206, WAMR46634-5.
- Pogona minor 'minima' morphs: AMR133759, AMR133915, AMR133988, AMR136236, AMR136239; NMVD772-4, NMVD2435, NMVD8002; SAMR22836; WAMR23812, WAMR37737, WAMR87461. Pogona minor minima: WAMR19501-16.
- Pogona minor mitchelli: AMR38712, AMR100912-5, AMR101470-1, AMR101550; SAMR1399-1400, SAMR1404, SAMR3436, SAMR3546, SAMR15622; NMVD999-1001; WAMR13066, WAMR15823, WAMR19377, WAMR45758-60, WAMR46068, WAMR50696, WAMR68983, WAMR79111-2, WAMR87344.
- Pagona nullarbor: SAMR5034, SAMR5437, SAMR14313A-B, SAMR14314, SAMR15570, SAMR18170, SAMR19807, SAMR20106, SAMR22290, SAMR23005, SAMR23029, SAMR23939-41, SAMR25298-301, SAMR26171, SAMR26393, SAMR26395; WAMR16888, WAMR16896, WAMR24655, WAMR28127, WAMR31964-5, WAMR91743, WAMR91831-2, WAMR91870, WAMR91924.
- Pogona vitticeps: AM field series 11252; AMR13904-5, AMR15296, AMR17122-3, AMR21077, AMR47319, AMR59991, AMR59996-7, AMR107398, AMR107406, AMR107409-10, AMR107444; NMVD648, NMVD699-700, NMVD777, NMVD787, NMVD970, NMVD1031, NMVD1036, NMVD1123, NMVD3072, NMVD7871, NMVD8970, NMVD11753-4, NMVD12164, NMVD14181, NMVD15379, NMVD15382, NMVD1820, NMVD47853, NMVD53853, NMVD52088-9, NMVD52637, NMVD52742, NMVD53482, NMVD53827, NMVD53856, NMVD53853, NMVD53907, NMVD52637, NMVD54051, NMVD54070-1, NMVD54123, NMVD53836, NMVD53853, NMVD53907, NMVD54749, NMVD54754, NMVD54779, NMVD54123, NMVD54131-2, NMVD54144, NMVD54577, NMVD54749, NMVD54754, NMVD54759, 60, NMVD54789-90, NMVD55036, NMVD55064, NMVD55251, NMVD55305, NMVD5583, NMVD56741, NMVD58472, NMVD58477, NMVD58501, NMVD58548, NMVD58555, NMVD58570, NMVD59448, NMVD59818, NMVD60324-5, NMVD60609, NMVD60694-5, NMVD60708, NMVD60741, NMVD59448, NMVD59848, NMVD60768-9, NMVD60778, NMVD60785, NMVD60785, NMVD60826-8, NMVD60841, NMVD60854, NMVR4547-8, NMVR4855, NMVR13781-2.
- Ctenophorusnuchalis: AM field series 11228, 11327, 11329-31; AMR542, AMR2113-4, AMR4892, AMR7024, AMR9540, AMR10873-5, AMR11924, AMR11928-30, AMR11936, AMR11938, AMR11943, AMR11946, AMR11954-5, AMR11981, AMR11983, AMR13911-3, AMR13918, AMR13920, AMR13925, AMR17260, AMR17610, AMR21466-9, AMR107377-81.
- Amphibolurus norrisi: NMVD14804-5, NMVD51499, NMVD51507, NMVD51576, NMVD51608, NMVD51617, NMVD51729, NMVD51752, NMVD51759, NMVD51763, NMVD51765, NMVD51771, NMVD52550, NMVD52557, NMVD52662, NMVD52632, NMVD52677, NMVD52693, NMVD52996, NMVD53057, NMVD53072, NMVD53077, NMVD53470, NMVD53488, NMVD53501, NMVD53854-5, NMVD53916, NMVD54119, NMVD54150, NMVD54152, NMVD54154, NMVD54202, NMVD55606.